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REPELLENCY OF SUCROSE TO CAPTIVE AMERICAN ROBINS

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Abstract: American robins (*Turdus migratorius*) are often pests of commercial fruit crops in North America. Because robins lack sucrase and cannot digest sucrose, they may develop an aversion to high-sucrose fruits. Thus, I tested captive robins with aqueous solutions of 15% (g/mL) mixed sugars (x% sucrose + y% glucose and fructose mixture = 15% sugar) to identify the level of sucrose required to develop a conditioned feeding aversion when digestible sugars are present. In 1-tube tests, robins decreased intake of 15% sucrose solutions 50% below baseline, but maintained stable intake of 3.75% and 7.5% sucrose solutions. In 2-tube tests with sucrose solutions paired against a glucose-fructose solution, robins avoided the 15% treatment in the first hour of testing ($P < 0.05$), yet were indifferent in the full 4-hour test ($P > 0.05$). My data suggest that a fruit cultivar would require as much as 15% sucrose to repel robins, and such high sugar concentrations naturally occur in fruits. Development of high sucrose cultivars would require almost complete replacement of simple sugars by sucrose and might be possible through selective breeding.

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American robins and European starlings (*Sturnus vulgaris*) damage small-berried fruit crops such as cherries, grapes, and blueberries (Stone 1973, Mott and Stone 1973, DeHaven 1974, Nelms et al. 1990). At maturity each of these fruits has low concentrations (<1%) of the fruit sugar, sucrose (Whiting 1970). Both bird species lack the digestive enzyme sucrase, which is required to hydrolyze the disaccharide sucrose (Martínez del Rio et al. 1988, Karasov and Levey 1990). When these birds consume sucrose, digestive upset and osmotic imbalance ensue (Schuler 1983, Martínez del Rio and Stevens 1989).

Consumption of sucrose by sucrase-deficient species may elicit a conditioned feeding aversion (Martínez del Rio 1990). Thus, increasing the sucrose content may reduce fruit damage by creating secondary repellency through post-ingestional distress (Rogers 1974, Brugger and Nelms 1991). Tests with starlings (Schuler 1983, Martínez del Rio et al. 1988) and robins (Brugger and Nelms 1991) suggest that feeding aversions develop when sucrose is offered against an unflavored alternative. It is not known, however, whether sucrase-deficient birds reject solutions of sucrose when they are supplemented with other digestible sugars or when they are offered with digestible sugars as an alternative. Glucose or fructose could affect food choice by mitigating the negative physiological effects of sucrose in the digestive tract. Thus, the mixture of 3 sugars, as is found in many fruits, may result in drinking responses that are different from those previously observed when sucrose alone was offered with water.

In this study, I assessed the potential for developing bird-deterrent, high-sucrose fruit cultivars by identifying the feeding responses of sucrase-deficient robins to variable doses of sucrose in the presence of digestible sugars. My objectives were to determine whether robins developed aversions to sucrose when it was mixed with the digestible sugars glucose and fructose; and whether drinking preferences were present when 2 choices of aqueous solutions were offered, one entirely digestible (glucose and fructose) versus one only partially digestible (sucrose, glucose, and fructose).

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METHODS

Birds

Robins were captured with mist nets during February 1991 in Alachua County, Florida, and kept in an outdoor aviary in 1.3- × 1.3- × 1-m cages with <6 birds/cage for a minimum of 2 weeks prior to testing. Robins were fed a mashed banana diet (Denslow et al. 1987), supplemented with mealworm larvae (*Tenebrio* spp.), and given water ad libitum during the period of acclimation and testing.

Test Sugars

I studied fructose (F), glucose (G), and sucrose (S) because they occur naturally in fruits at modal concentrations that range from 10 to 15% (g/mL, Whiting 1970). All test solutions were 15% total sugar, but varied in their concentrations of indigestible sugar (sucrose) and digestible sugars (glucose, fructose). In all experiments, I used glucose and fructose in a 1:1 ratio because most small-berried fruits typically contain such equal proportions (Whiting 1970).

I tested 3 sugar treatments: 3.75% S + 11.25% GF, 7.5% S + 7.5% GF, and 15% S, and I used a control solution (15% GF) to identify baseline consumption of digestible sugars. I obtained fructose (CAS # 57-48-7), glucose (CAS # 50-99-7), and sucrose (CAS # 57-50-1) from Sigma Chemical Company, St. Louis, Missouri. I mixed solutions in glassware with distilled water.

Experimental Design

Prior to testing, I moved birds from their holding cages to individual 60- × 60- × 90-cm cages. After 1 week of acclimation, birds experienced a 3-day training period to learn to drink from glass tubes containing the 15% GF mixture. The procedures were similar among training, pretest, and test days. Each day, I removed the maintenance food and water from the cage at 0900 (2 hr after sunrise). At 1000 I offered individual robins glass drinking tube(s) that contained the test solution(s) and placed aluminum pans under the cages to collect feces and urine. At hourly intervals until 1400, I measured fluid consumption from each tube to the nearest mm and transformed the value to volume units. Using a pocket refractometer, I measured the sugar concentrations of 3 fecal samples from each bird 1 hour after testing began to estimate the proportion of nonabsorbed sugar defecated from the gut (Hainesworth 1974, Bolten et al. 1979). The pans were not sampled after the first hour because I could not be sure which droppings were fresh. Maintenance food and water were replaced in the cages by 1500.

One-Tube Test.—I used a 4-day, 1-tube design to test for physiological tolerance to sucrose mixed with digestible sugars. I gave robins 15% GF in a single tube on days 1 and 2 to determine baseline intake, and offered the sucrose solutions on days 3 and 4.

Two-Tube Test.—I used a 5-day, 2-tube design to test for aversion to a sucrose solution when offered with an entirely digestible alternative sugar solution. I added a third day to the treatment period to allow fuller expression of preferences than that of a 2-day test. I used 2 concentrations of sucrose (7.5% and 15%) and 10 birds/treatment. I dropped the 3.75% S solution from the 2-tube test because robins readily consumed it in the 1-tube tests, suggesting possible indifference to it. I presented the test solutions to individual robins in 2 glass drinking tubes 10 cm apart at the back of the cage. On days 1 and 2, I offered only the GF mixture in each tube to obtain baseline consumption. On days 3 to 5, I offered a sucrose solution in 1 tube and the GF solution in the other. I randomly selected the position (right or left) of the sucrose solution for each bird and kept that location throughout the test period (Pick and Kare 1962).

Statistics

Analyses were run on a Macintosh SE/30 with the SYSTAT software package (Wilkinson 1990). Prior to analyses, all dependent variables were tested for equality of variances among cells using Bartlett's test. I transformed preference ratios and fecal sugar concentrations with the arcsin square root transformation and intake with a $\log_{10}$ transformation to meet assumptions of ANOVA and t-tests (Sokal and Rohlf 1981). I analyzed data from the first hour separately from the total 4-hour test period because robins might have responded differently when first given the sugar solutions than 4 hours later, when they might have sampled the tubes out of boredom, hunger, or lack of alternative food. In both experiments, I predicted that total intake would decrease and fecal sugar concentration increase with increased sucrose concentrations. I used linear and nonlinear regressions to test for relationships of total intake, sucrose intake, sucrose preference, and fecal sugar concentration.

I used a 2-way ANOVA to test for differences in dependent variables (mean intake and fecal sugar concentrations) among sucrose concentrations (3.75, 7.5, and 15%) and between periods (pretest vs. test). I interpreted that a feeding aversion occurred if a significant period effect was detected. I present results of the 2-way ANOVA in the text, yet provide figures with

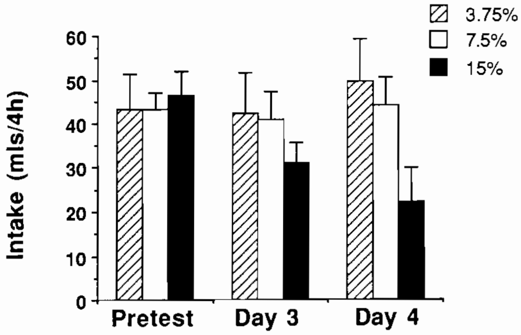

Fig. 1. Mean (±SE) fluid consumption by American robins given aqueous solutions of 15% mixed sugars in 1-tube tests conducted in Gainesville, Florida, March 1991. Pretest solutions were 1:1 glucose : fructose. Test solutions contained sucrose (3.75, 7.5, or 15%) and 1:1 glucose : fructose. Sample size was 8 birds/treatment.

combined pretest responses and daily test responses of robins to illustrate temporal trends.

I calculated a sucrose preference ratio for individual robins with the equation,

$$\text{Preference ratio} = \frac{\text{(consumption of sucrose solution)}}{\text{(consumption of both solutions)}}$$

(Kare et al. 1957). I predicted that robins would avoid sucrose solutions and that the sucrose preference ratios would decrease with increasing sucrose concentration. I used a single sample t-test to test the null hypothesis that mean sucrose preference did not differ from 0.5. I interpreted that a feeding aversion occurred if sucrose preference ratios were significantly less than 0.5.

RESULTS

One-Tube Tests

Mean 4-hour intake did not vary due to sucrose concentration ($F_{2,90} = 0.30$, $P = 0.74$), but the effects of test period ($F_{2,90} = 4.21$, $P = 0.04$) and interaction of sucrose concentration and test period ($F_{2,90} = 4.70$, $P = 0.01$) were significant. Consumption did not differ between pretest and test periods in the 3.75% and 7.5% sucrose groups, averaging 42.4 (SE = 4.8) mL/4 hours, but was on average 50% lower in the 15% sucrose treatment than the pretest level (Fig. 1). Results obtained in the first-hour were similar to those of the 4-hour test. In the 3.75% and 7.5% treatments, robins consumed <3.3 g sucrose each day; in the 15% treatments, robins consumed

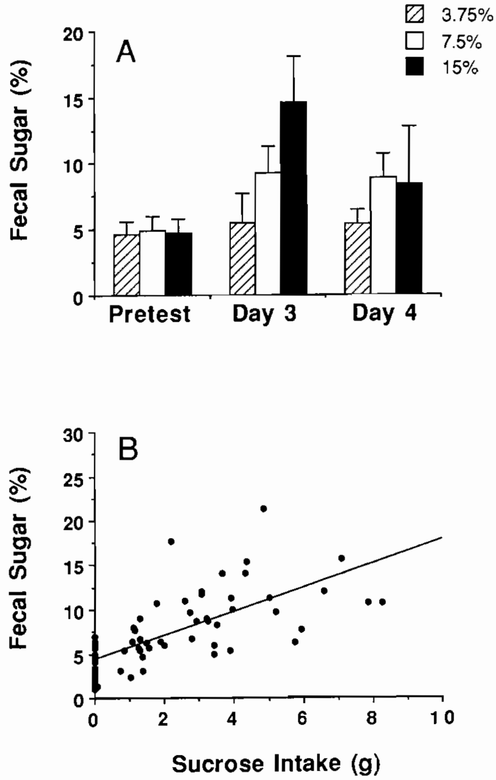

Fig. 2. Fecal sugar concentrations (%) of American robins after 1 hour of drinking 3.75, 7.5, or 15% sucrose solutions during tests conducted in Gainesville, Florida, March 1991. (A) Mean (±SE) fecal sugars from 2 pretest days combined and individual test days. Pretest solutions were 1:1 glucose : fructose. (B) Relationship of fecal sugar concentration (%) to sucrose intake (g) after 1 hour of drinking mixed sugar solutions.

<3.3 g sucrose each day; in the 15% treatment, they consumed an average of 4.8 g sucrose on day 3 and 3.45 g on day 4.

Mean fecal sugar concentrations varied as an effect of sucrose concentration ($F_{2,63} = 31.66$, $P < 0.001$), test period ($F_{2,63} = 14.07$, $P < 0.001$) and the interaction of sucrose concentration and test period ($F_{2,63} = 7.74$, $P < 0.001$). Fecal sugars increased above baseline on the day sucrose solutions were offered, and increased with increasing sucrose concentration (day 3, Fig. 2A). Within treatments, mean fecal sugar concentrations decreased slightly the second day sucrose solutions were given (day 4, Fig. 2A). The fecal sugar concentration of individual robins was related to the mass (g) of sucrose consumed (Fig. 2B). The regression of first-hour fecal sugar (y) on first-hour sucrose intake (x) yielded the equation, $y = 4.33 + 1.35x$ ($r^2 = 0.49$, 69 df, $P < 0.001$).

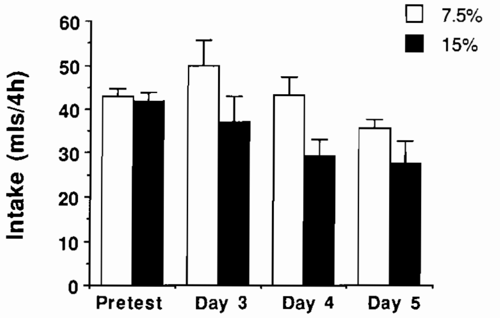

Fig. 3. Mean (±SE) fluid consumption by American robins given aqueous solutions of 15% mixed sugars in 2-tube tests conducted in Gainesville, Florida, March 1991. Pretest solutions were 1:1 glucose : fructose. Test solutions contained sucrose (7.5% or 15%) and 1:1 glucose : fructose. Sample size was 10 birds/treatment.

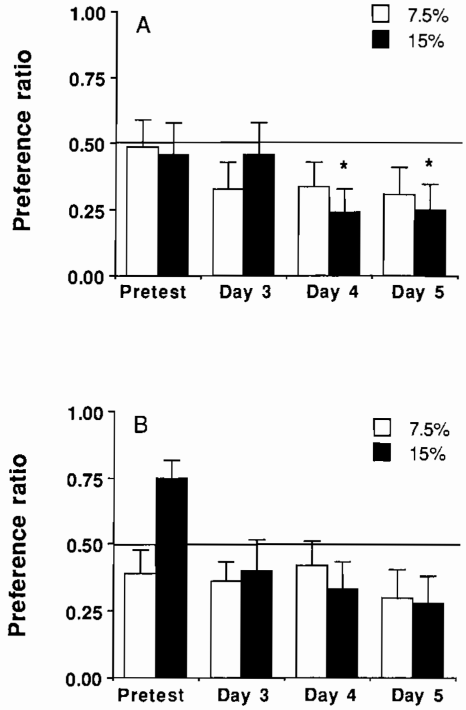

Fig. 4. Preference ratios of American robins for 7.5% or 15% sucrose solutions in 2-tube tests with 15% 1:1 glucose : fructose as the alternate solution. Data are from tests conducted in Gainesville, Florida, March 1991. Pretest solutions were 1:1 glucose : fructose. (A) Preference ratios calculated from the first hour of testing; * = values differed from 0.5. (B) Preference ratios calculated from 4 hours of testing. Indifference is inferred if values do not differ from 0.5, a preference if values exceed 0.5, and avoidance if values are less than 0.5.

Two-Tube Tests

Mean intake during 4 hours varied as an effect of sucrose concentration ($F_{1,96} = 5.42$, $P = 0.02$), but not as an effect of test period ($F_{1,96} = 1.34$, $P = 0.25$) or an interaction of sucrose and test period ($F_{1,96} = 1.94$, $P = 0.17$). Robins in the 15% sucrose treatment group consistently drank less fluid than those in the 7.5% treatment. Total intake tended to decline throughout the test period (days 3–5) in both treatment groups (Fig. 3). Total fluid intake by birds in the 15% treatment may have declined among days in relation to the amount of sucrose consumed ($r^2 = 0.19$, 29 df, $P = 0.02$). Intake during the first hour was similar to that of the 4-hour test.

The pattern of sucrose preferences differed between treatment groups depending on whether 1-hour or 4-hour data were used to calculate preference ratios. Robins in the 7.5% treatment groups had decreased preference ratios during the 3 test days, but were indifferent to the sucrose solution throughout the test ($P > 0.05$, Fig. 4). Robins in the 15% treatment group avoided the sucrose solution in the first hour of testing on days 4 and 5 ($P < 0.05$, Fig. 4A), but were indifferent during 4 hours of testing ($P > 0.05$, Fig. 4B). By chance during the pretest, robins in the 15% treatment had high preferences for the tube that later held sucrose. Thus, preferences were suppressed relative to pretest levels, but not significantly below a null value of 0.5.

Fecal sugars did not differ among days in the 7.5% treatment ($P > 0.05$), but they declined among days in the 15% treatment among individuals ($P < 0.05$). Fecal sugars were related to sucrose intake during the first hour of testing ($r^2 = 0.10$, 79 df, $P < 0.01$) and to sucrose preference ratios ($r^2 = 0.36$, 59 df, $P < 0.001$), but not to first-hour fluid intake.

DISCUSSION

American robins appear unable to digest sucrose, whether consumed alone or consumed with digestible sugars. Although this was predicted upon the discovery of sucrase deficiency in 5 robins (Karasov and Levey 1990), the question remained as to whether there could be variation in the presence of the disaccharidase in a larger sample of robins. My data demonstrate a direct relationship between percent solutes in feces and sucrose intake (Fig. 2) and suggest that all robins lack sucrase. Variation about the regression line probably results, in part, from the amount of water the robins were excreting and the presence of other solutes in the droppings, such as uric acid, which refract light and increase the measure (Inouye et al. 1980).

For palatable substances, post-ingestional distress could be a necessary precondition to developing a feeding aversion. Sucrose, consumed in sufficient quantity by sucrase deficient animals, causes osmotic imbalance due to uncleaved molecules remaining within the intestine and attracting water into the lumen from other somatic compartments (Dahlqvist 1962). After the 1-tube 15% sucrose tests, several birds exhibited behavior that was symptomatic of osmotic imbalance; they were inactive, had dissheveled plumage, and perched in slumped or listing postures. When water and food were replaced in the cages, these birds perched by their water cups, and drank continuously for up to 45 minutes (K. E. Brugger, unpubl. data). The decreased intake of the sucrose solution on the following day suggested that somatic dehydration and gastrointestinal bloating were sufficiently stressful to elicit a feeding aversion.

How much sucrose must a robin consume to create a feeding aversion? Osmotic pressure in the intestinal lumen might have to exceed that of the body to elicit sucrose avoidance. Thus, the amount of sucrose ingested, the rate of ingestion, the presence of other food in the gut, and environmental factors such as ambient temperature, humidity, or availability of free water for drinking may influence the development of an osmotically-based, learned food aversion.

In 1-tube tests, I found that robins required 3.3–5.0 g sucrose in 4 hours and 1 prior exposure to the sucrose-enriched solutions before an aversion developed. Only the 15% treatment provided sufficient sucrose to promote the aversion. In 2-tube tests, I obtained partial support for the prediction that robins would avoid sucrose solutions. Preferences declined over 3 days in the 15%, but not the 7.5% treatment. This suggests that robins can distinguish between the sucrose and monosaccharide solutions. These data also suggest that under field conditions, robins might require several days of sampling fruits before they learn to avoid high-sucrose crops, especially if they are consuming a mixed diet or have access to water.

MANAGEMENT AND RESEARCH IMPLICATIONS

My data suggest that fruits would require as much as 15% sugar by mass and a relatively large proportion of that sugar must be sucrose to repel robins. Possibly, a threshold concentration occurs between 7.5 and 15% sucrose beyond which consumption, and therefore fruit damage, would decrease. Fruits contain sugar concentrations that range from extremes of 5 to 20%, depending on factors such as genetic stock, rates of photosynthesis, and rainfall during maturation (Whiting 1970). Thus, development of a high-sucrose cultivar with a potential for bird deterrency appears attainable.

Fruits can be classified as sucrose metabolizers (cherries, grapes, blueberries) or sucrose accumulators (citrus, melons, apricots), depending on whether translocated sucrose is broken down to glucose and fructose by enzymes in the ripening fruit (Willenbrink 1982). Natural variation in sucrose concentration occurs in some small-berried fruits (Whiting 1970). If sucrose metabolism in cherries, grapes, or blueberries can be understood, then selective replacement of fructose and glucose by sucrose might be obtained through plant breeding or cloning techniques. It is reasonable to pursue development of a high-sucrose cultivar for use in reduction of bird damage for 3 reasons. Robins respond to sucrose at a total sugar concentration that naturally occurs in fruits (≤15% w/vol). Humans find sucrose palatable and digestible, and prefer its taste to that of glucose or fructose (Vettorazzi and MacDonald 1988). Sucrose is a natural constituent of fruits and thus offers a nonlethal means for repelling birds in orchards and fields.

Research is needed in the following areas to develop this integrated pest management strategy for birds that feed in fruit crops: avian physiology (especially how birds detect, digest, and metabolize carbohydrates); avian behavioral ecology; and the relationship of fruit quality to plant genetics. Integration of information concerning avian physiology and fruit chemistry with knowledge of avian feeding behavior would help identify potential feeding responses of birds to new cultivars. For example, if robins must feed for several days in high-sucrose cultivars to develop an aversion, then the technique might be useful to deter resident populations, but not short-term migrants. Alternatively, if the presence of other food in the gut reduces the aversiveness of sucrose, then perhaps widespread planting of a high-sucrose cultivar would be required for deterrence. Further research also is needed to determine the associative effects of sucrose and other dietary components on osmotic balance in birds that lack sucrase. Improvement of our understanding of the factors that regulate sucrose in maturing fruits, and the relationship of sucrose concentration to fruit quality, would help identify feasibility of developing high-sucrose cultivars for bird deterrence from an agricultural standpoint. My data suggest that almost complete replacement of glucose and fructose by sucrose would be required to attain a fruit cultivar that can be tested for avian repellency in field trials. Refinement of the estimate requires additional testing of a series of treatments between 7.5% and 15% sucrose.

LITERATURE CITED

BOLTEN, A. B., P. FEINSINGER, H. G. BAKER, AND I. BAKER. 1979. On the calculation of sugar concentration in flower nectar. Oecologia 41:301–304.

BRUGGER, K. E., AND C. O. NELMS. 1991. Sucrose avoidance by American robins (*Turdus migratorius*): implications to control of bird damage to fruit crops. Crop Prot. 10:455–460.

DAHLQVIST, A. 1962. The intestinal disaccharidases and disaccharide intolerance. Gasteroenterology 43:694–696.

DEHAVEN, R. W. 1974. Bird damage to wine grapes in central California, 1973. Proc. Vertebr. Pest Conf. 6:248–252.

DENSLOW, J. S., D. J. LEVEY, T. C. MOERMOND, AND B. C. WENTWORTH. 1987. A synthetic diet for fruit-eating birds. Wilson Bull. 99:131–135.

HAINESWORTH, F. R. 1974. Food quality and foraging efficiency: the efficiency of sugar assimilation by hummingbirds. J. Comp. Physiol. 88: 425–431.

INOUYE, D. W., N. D. FAVRE, J. A. LANUM, D. M. LEVINE, J. B. MEYERS, M. S. ROBERTS, F. S. TSAO, AND Y. Y. WANG. 1980. The effects of nonsugar constituents on estimates of nectar energy content. Ecology 61:992–996.

KARASOV, W. H., AND D. J. LEVEY. 1990. Digestive tradeoffs and adaptations for frugivorous birds. Physiol. Zool. 63:1248–1270.

KARE, M. R., R. BLACK, AND E. G. ALLISON. 1957. The sense of taste in the fowl. Poult. Sci. 36:129–138.

MARTÍNEZ DEL RIO, C. 1990. Dietary, phylogenetic, and ecological correlates of intestinal sucrase and maltase activity in birds. Physiol. Zool. 63: 987–1011.

———, AND B. R. STEVENS. 1989. Physiological constraint on feeding behavior: intestinal membrane disaccharidases of the starling. Science 243: 794–796.

———, ———, D. E. DANEKE, AND P. T. ANDREADIS. 1988. Physiological correlates of preference and aversion for sugars in three species of birds. Physiol. Zool. 61:222–229.

MOTT, D. F., AND C. P. STONE. 1973. Bird damage to blueberries in the United States. U.S. Fish and Wildl. Serv. Spec. Sci. Rep. 172. 15pp.

NELMS, C. O., M. L. AVERY, AND D. G. DECKER. 1990. Assessment of bird damage to early-ripening blueberries in Florida. Proc. Vertebr. Pest Conf. 14:302–306.

PICK, H. L., AND M. R. KARE. 1962. The effect of artificial cues on the measurements of taste preference in the chicken. J. Comp. Physiol. Psychol. 55:342–345.

ROGERS, J. G., JR. 1974. Responses of caged red-winged blackbirds to two types of repellents. J. Wildl. Manage. 38:418–423.

SCHULER, W. 1983. Responses to sugars and their behavioral mechanisms in the starling (*Sturnus vulgaris*). Behav. Ecol. Sociobiol. 13:243–251.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. Second ed. W. H. Freeman and Co., San Francisco, Calif. 869pp.

STONE, C. P. 1973. Bird damage to tart cherries in Michigan, 1972. Proc. Bird Control Semin. 6:19–23.

VETTORAZZI, G., AND I. MACDONALD. 1988. Sucrose: nutritional and safety aspects. Springer-Verlag, New York, N.Y. 192pp.

WHITING, G. C. 1970. Sugars. Pages 1–31 *in* A. C. Hulme, ed. The biochemistry of fruits and their products. Academic Press, New York, N.Y.

WILKINSON, L. 1990. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, Ill. 248pp.

WILLENBRINK, J. 1982. Storage of sugars in higher plants. Pages 684–699 *in* F. A. Loewus and W. Tanner, eds. Encyclopedia of plant physiology. Springer-Verlag, New York, N.Y.

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